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Recovery Potential Modelling of Western Silvery Minnow (*Hybognathus argyritis*) in Canada

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Canada

Foreword

This series documents the scientific basis for the evaluation of aquatic resources and ecosystems in Canada. As such, it addresses the issues of the day in the time frames required and the documents it contains are not intended as definitive statements on the subjects addressed but rather as progress reports on ongoing investigations.

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ABSTRACT

The Committee on the Status of Endangered Wildlife in Canada (COSEWIC) had assessed the Western Silvery Minnow (*Hybognathus argyritis*) as Endangered in Canada (2008). Here we present population modelling to assess allowable harm, determine population-based recovery targets, and conduct long-term projections of population recovery in support of a recovery potential assessment (RPA). Our analyses demonstrated that the dynamics of Western Silvery Minnow populations are particularly sensitive to perturbations that affect survival of immature individuals (from hatch to age 2), or the fecundity of first time spawners. Harm to these portions of the life cycle should be minimized to avoid jeopardizing the survival and future recovery of Canadian populations. Based on an objective of demographic sustainability (i.e., a self-sustaining population over the long term), we propose a population abundance recovery target of 12 000–236 000 adult Western Silvery Minnow, requiring 25–497 ha of suitable habitat. In the absence of mitigating efforts, additional harm or habitat limitations, we estimate that a growing Western Silvery Minnow population will take approximately 9 years to reach this recovery target if starting from a population of 1200 adults. Recovery strategies which incorporate improvements in the most sensitive vital rates of the Western Silvery Minnow will have the greatest effect on population growth.

Modélisation du potentiel de rétablissement du méné d'argent de l'Ouest (*Hybognathus argyritis*) au Canada

RÉSUMÉ

Le Comité sur la situation des espèces en péril au Canada (COSEPAC) a évalué le méné d'argent de l'Ouest (*Hybognathus argyritis*) comme étant une espèce en voie de disparition au Canada (2008). Ce document présente la modélisation de la population afin d'évaluer les dommages admissibles, d'établir les objectifs de rétablissement en fonction de la population et d'effectuer des projections à long terme du rétablissement de la population en vue d'appuyer l'évaluation du potentiel de rétablissement (EPR). Nos analyses ont démontrées que la dynamique des populations du méné d'argent de l'Ouest est particulièrement sensible aux perturbations qui nuisent à la survie des individus immatures (de l'éclosion à l'âge 2) et à la fécondité des individus qui fraient pour la première fois. Il faut réduire le plus possible les dommages à ces stades du cycle de vie afin d'éviter de mettre en péril la survie et le rétablissement futur des populations au Canada. En nous basant sur un objectif de durabilité démographique (c.-à-d. une population autonome à long terme), nous proposons une cible de rétablissement de l'abondance d'entre 12 000 et 236 000 ménés d'argent de l'Ouest, qui auront besoin de 25 à 497 ha d'habitat convenable. En l'absence d'efforts d'atténuation, de dommages supplémentaires ou de restrictions en matière d'habitat, nous estimons qu'il faudra attendre 9 ans pour qu'une population croissante de ménés d'argent de l'Ouest atteigne l'objectif de rétablissement, si l'on commence avec une population de 1 200 adultes. Ce sont les programmes de rétablissement visant une amélioration des indices vitaux les plus sensibles du méné d'argent de l'Ouest qui auront la plus grande incidence sur la croissance de la population.

INTRODUCTION

The Western Silvery Minnow (*Hybognathus argyritis*), is typically found in the plains in quiet water with low velocity, and in Canada is found only in the Milk River in Alberta. Due to its limited distribution, the Western Silvery Minnow may be particularly susceptible to threats such as siltation, changes in water flows and levels, prolonged drought, and introduced pollutants. The Western Silvery Minnow was first designated as a species of Special Concern in 1997, re-assessed as Threatened in 2001, and assessed as Endangered in 2008.

In accordance with the *Species at Risk Act* (SARA), which mandates the development of strategies for the protection and recovery of species that are at risk of extinction or extirpation in Canada, Fisheries and Oceans Canada has developed the recovery potential assessment (RPA; DFO 2007) as a means of providing information and scientific advice. There are three components to each RPA: an assessment of species status, the scope for recovery, and scenarios for mitigation and alternatives to activities (DFO 2007). This last component requires the identification of recovery targets and timeframes for recovery, and measures of uncertainty associated with the outcomes of recovery efforts. Here, we contribute to components two and three by assessing allowable harm, identifying recovery targets, projecting recovery timeframes and identifying mitigation strategies for Canadian populations of Western Silvery Minnow. This work is based on a demographic approach developed by Vélez-Espino and Koops (2007, 2009a, 2009b), which uses a population-based recovery target, and provides long-term projections of population recovery under a variety of feasible recovery strategies.

METHODS

Our analysis consisted of four parts: (i) information on vital rates was compiled and used to build projection matrices, using uncertainty in life history to represent variation in the life cycle for stochastic simulations; (ii) we used these matrices in a stochastic perturbation to determine the sensitivity of the population growth rate to changes in each vital rate, as well as to determine allowable harm. Following Vélez-Espino and Koops (2007, 2009a, 2009b); (iii) the projection matrices were used to simulate risk of extinction, and to estimate the minimum viable population (MVP); and (iv) using the MVP as a recovery target, we simulated the effects of potential recovery efforts on time to recovery of a typical population. The effects of habitat limitations and associated density dependence were explored.

SOURCES

Where possible, life history estimates for the Western Silvery Minnow were based on sampling data from Canadian populations in the Milk River, Alberta, between 2005 and 2007 (D. Watkinson, DFO unpublished data).

MATRIX MODEL

Using a matrix approach, the life cycle of Western Silvery Minnow was represented with annual projection intervals and by a post-breeding age-structured projection matrix (Caswell 2001; Figure 1). Individuals were assumed to first mature at age 2, and reach a maximum age of 4 years (see following section). The model therefore represents five age classes: young of the year (age 0), juveniles (age 1) and 3 adult age classes.

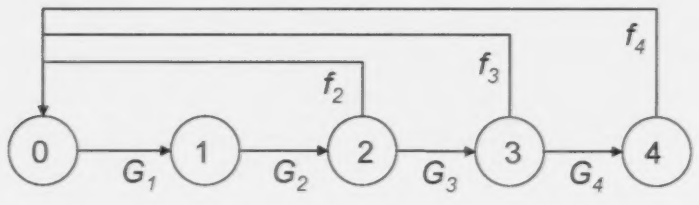
Elements of the age-structured matrix included the fecundity coefficient of age class j (F_j), and the age specific annual survival probability from age j-1 to age j (G_j). Fecundity coefficients (F_j) represent the contribution of an adult in age class j to the next census of age-0 individuals.

Since a post-breeding model is assumed, the coefficient F_j includes the annual survival probability of adults from age j-1 to age j, as well as the age-specific fertility upon reaching age j (f_j) such that

$$F_j = G_j f_j \quad (1)$$

where f_j is the product of a stage's average number of eggs (m_j), the proportion of females (assumed to be 50%), and the inverse of the average spawning periodicity (assumed to be 1).

a)



b)
$$M = \begin{pmatrix} 0 & F_2 & F_3 & F_4 & 0 \\ G_1 & 0 & 0 & 0 & 0 \\ 0 & G_2 & 0 & 0 & 0 \\ 0 & 0 & G_3 & 0 & 0 \\ 0 & 0 & 0 & G_4 & 0 \end{pmatrix}$$

c)
$$M = \begin{pmatrix} 0 & 376 & 1022 & 1598 & 0 \\ 0.011 & 0 & 0 & 0 & 0 \\ 0 & 0.21 & 0 & 0 & 0 \\ 0 & 0 & 0.30 & 0 & 0 \\ 0 & 0 & 0 & 0.35 & 0 \end{pmatrix}$$

Figure 1. Generalized life cycle (a), corresponding age-structured projection matrix (b), and mean values of matrix elements (c) used to model the population dynamics of Western Silvery Minnow. F_i represents fecundities, and G_i the survival probabilities from age j-1 to age j. Note that fertility is positive for the age 1 class (F_2) since individuals recorded as age 1 in census t will mature upon their second birthday (if they survive) and produce offspring that will be counted at census t+1 (Caswell 2001).

Parameter Estimates

To estimate parameters for the matrix model (summarized in Table 1) we first established a mean size for each age class. Western Silvery Minnow collected from the Milk River were aged using fin rays (n=30), and a von Bertalanffy growth curve was fitted to these data (Figure 2). The von Bertalanffy growth curve relates size and age with the formula $L_t = L_\infty(1 - e^{-k(t-t_0)})$, where L_t is size at time t, t_0 is the age at which the fish would have had length 0, L_∞ is the asymptotic size, and k is a growth parameter. This fit gave a negative size for age-0 fish. Since we know fry to be approximately 6 mm upon hatching (Scott and Crossman 1973), we re-fit the curve with the assumption that it passes through 6 mm at age 0. This yielded estimates of L_∞ =

120.5, k = 0.574 and t_0 = -0.04. Uncertainty in mean size-at-age was incorporated by calculating bootstrapped confidence intervals on the fitted growth curve (Baty and Delignette-Muller 2009).

*Table 1. Mean and standard deviation of vital rates for Western Silvery Minnow. G_j = annual survival probability from age j-1 to age j. f = annual number of female offspring (multiply by 2 for total) *Used for calculating minimum viable population (MVP).*

		Survival (G_j)		Fecundity (f)	
age	Fork Length (mm)	mean	sd	mean	sd
1	56	0.011	0.007	0	NA
2	84	0.207	0.046	1815	197
3	100	0.302	0.051	3383	222
4	109	0.347	0.052	4607	320
1 (adjusted)*	NA	0.0014	0.007	NA	NA

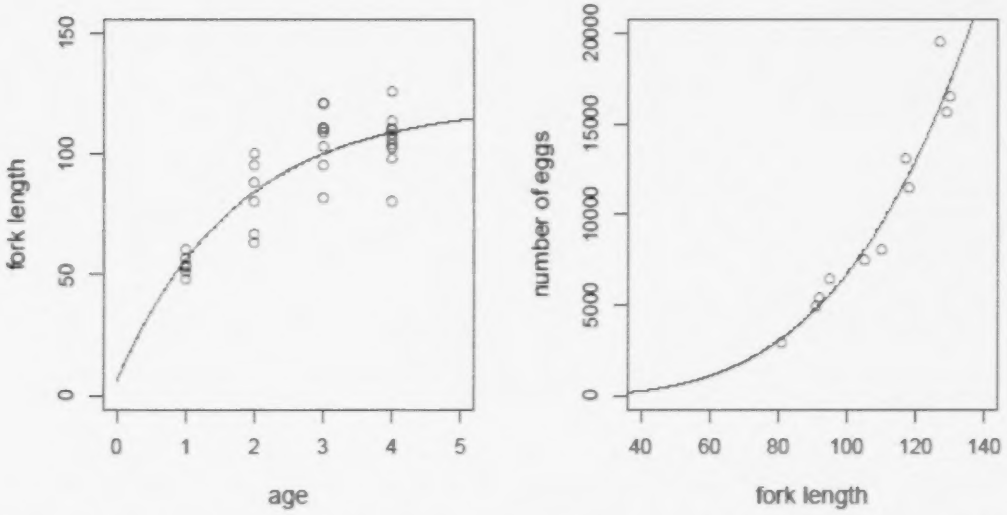


Figure 2. Sample data collected from Western Silvery Minnow in the Milk River. Left: Von Bertalanffy growth curve, fitted to size-at-age data. Right: size-specific fecundity (total number of eggs) with fitted exponential curve.

Fecundity was described as a function of fork length (FL) by performing log-linear regression (Figure 2; $\ln(f)=7.79 - 3.61 \cdot \ln(FL) - 4.1$; $R^2=0.96$, p=0.96, n=11). Mean fecundity for each age-class was calculated using mean size-at-age, and multiplied by the sex ratio (0.5). Uncertainty in fecundity incorporated both uncertainty in size-at-age (using confidence intervals from the von Bertalanffy growth curve), and uncertainty in fecundity-at-size (using confidence intervals of the log-linear fecundity regression). The combined uncertainty bounds were assumed to contain all possible fecundity values within 4 standard deviations of the mean (i.e., variance was calculated assuming that the range of uncertainty was a 95% confidence interval).

Size-dependent mortality was estimated by combining a size-dependent mortality model (Lorenzen 2000) with von Bertalanffy growth parameters and a catch curve analysis of age-frequency data (Hilborn and Walters 1992). The ages of un-aged fish were calculated based on their lengths, using the fitted von Bertalanffy growth curve above. Mortality was assumed to decline proportionally with increases in size (Lorenzen 2000) such that

$$M_t = \frac{m_0}{L_t}, \quad (2)$$

where M_t and L_t are the instantaneous mortality and mean length at time t, and m_0 is the mortality at unit size (i.e., at $L_t = 1$). If L_t is described by the von Bertallanffy growth curve equation, survival from age j to age j+1 can be calculated by integrating equation (2) and evaluating between j and j+1:

$$s_{j,\,j+1} = \left[\frac{L_j e^{-k}}{L_{j+1}}\right]^{m_0/kL_\infty}. \quad (3)$$

k and L_∞ are parameters of the von Bertalanffy growth equation as evaluated above. The parameter m_0 can be estimated by performing a modified catch curve analysis where logged frequencies are binned based on equation (4), so that m_0 can be described by the slope of the catch curve regression (β), scaled by the von Bertalanffy parameters (equation 5).

$$\ln L_t + kt \quad (4)$$

$$m_0 = -kL_\infty\beta \quad (5)$$

Weighted catch curve regressions were performed to decrease the bias from rarer, older fish (Maceina and Bettoli 1998, Freund and Littell 1991). Survival from stage j to stage j+1 was calculated using equation (3). Variance for each survival rate was approximated by first translating the standard error of β from the catch curve regression into a standard error for m_0, then applying the delta method (Oehlert 1992) to equation (3) to estimate the variance of the transformed parameter. This process was repeated separately for sampling data from 2006 and 2007, and the averaged means and variances used for the model. Survival and fecundity rates for stochastic simulations were drawn from lognormal distributions with mean and variances as described above. Generation time was calculated from the age-specific survival and fecundity estimates as per Caswell (2001), and yielded a generation time of 2.6 years for the Western Silvery Minnow. Sampled Western Silvery Minnow were observed to be mature at 2 years, and live a maximum of 4 years.

ALLOWABLE HARM

We assessed allowable harm within a demographic framework following Vélez-Espino and Koops (2007, 2009a, 2009b). Briefly, we focused on estimates of annual population growth rate (λ) as determined by the largest eigenvalue of the projection matrix (Caswell 2001). Setting equilibrium (i.e., $\lambda = 1$) as the minimum acceptable population growth rate, allowable harm (τ_V) and maximum allowable harm ($\tau_{V,\,max}$) were estimated analytically as:

$$(6)\ \tau_v < \left(\frac{1}{\varepsilon_v}\right)\left(\frac{1-\Lambda}{\Lambda}\right) \text{ and } \tau_{v,\max} = \left(\frac{1}{\varepsilon_v}\right)\left(\frac{1-\Lambda}{\Lambda}\right)$$

where ε_v is the elasticity of vital rate v, and λ is population growth rate in the absence of additional harm (see below). Elasticities are a measure of the sensitivity of population growth rate to perturbations in vital rate v, and are given by the scaled partial derivatives of λ with respect to the vital rate:

$$(7) \qquad \varepsilon_v = \frac{v}{\lambda} \sum_{i,j} \frac{\partial \lambda}{\partial a_{ij}} \frac{\partial a_{ij}}{\partial v}.$$

Here, a_{ij} are the matrix elements.

In addition to calculating the elasticities of vital rates deterministically, as described above, we also incorporated variation in vital rates to determine effects on population responses from demographic perturbations. We used computer simulations (R, version 2.9.2: R Development Core Team 2009; code modified from Morris and Doak 2002) to (i) generate 5000 matrices, with vital rates drawn from distributions with means and variances as described above (see Vélez-Espino and Koops 2007); (ii) calculate λ for each matrix; (iii) calculate the ε_v of G_i and f_i for each matrix; and (iv) estimate mean stochastic elasticities and their parametric, bootstrapped 95% confidence intervals. For each vital rate, we then calculated maximum allowable harm for the mean, maximum (upper 95% CI), and minimum (lower 95% CI) values that were based on a mean λ of 2.3.

Because human activities often impact multiple vital rates simultaneously, we also used elasticities to approximate allowable simultaneous harm to survival or fertility rates. Cumulative harm was estimated as

$$(8) \qquad \Psi \approx \left(\frac{1 - \Lambda}{\Lambda} \right) \Big/ \sum_{v=1}^{n} \varepsilon_v$$

where n is the number of vital rates that are simultaneously harmed, ε_v is the elasticity of vital rate v, and ψ is allowable harm expressed as a single multiplier of all vital rates of interest.

RECOVERY TARGETS

We used demographic sustainability as a criterion to set recovery targets for Western Silvery Minnow. Demographic sustainability is related to the concept of a minimum viable population (MVP; Shaffer 1981), and was defined as the minimum adult population size that results in a desired probability of persistence (see below) over 100 years (approximately 38 generations). We estimated MVP for individual populations, not the species in total. To estimate MVP, we assumed discrete populations that function as demographically independent units (i.e., little or no immigration or emigration).

We estimated recovery targets as follows. (i) 50 000 projection matrices were generated using the means, variances, and distributions as in the allowable harm analysis, and based on a geometric mean growth rate of λ=1; (ii) projection matrices were drawn at random from these to generate 5000 realizations of population size per time step (i.e., over 100 years); (iii) these realizations were used to generate a cumulative distribution function of extinction probability, where a population was said to be extinct if it was reduced to one adult (female) individual; (iv) this process was repeated 10 times, giving an average extinction probability per time step. Catastrophic decline in population size, defined as a 50% reduction in abundance, was incorporated into these simulations, and occurred at a probability (P_k) 0.10 or 0.15 per generation (0.04% or 0.06% annually). We used these simulations to determine the number of adults necessary for the desired probability of persistence (see Results) over 100 years. For these simulations, mean age-0 survival was adjusted, with constant variance, so that the

population growth rate was at equilibrium (geometric mean of λ=1). This was done to simulate the probability of persistence of a stable population over the long term, since population growth is not sustainable over time.

MINIMUM AREA FOR POPULATION VIABILITY

Following Vélez-Espino *et al.* (2010), we estimated the minimum area for population viability (MAPV) as a first order quantification of the amount of habitat required to support a viable population. We calculated MAPV for each age-class in the population as:

$$(9) \qquad MAPV_j = MVP_j \cdot API_j$$

MVP_j is the minimum number of individuals per age-class required to achieve the desired probability of persistence over 100 years, as estimated for the recovery target. Individuals were distributed among age classes according to the stable age distribution, which is represented by the dominant right eigenvector (w) of the mean projection matrix ($\mathbf{M}\ w = \lambda \cdot w$) (De Kroon *et al.* 1986). The recovery target, MVP, is expressed in terms of adult numbers only (ages 2-4). API_j is the age-specific area required per individual (the inverse of density). We estimate API based on an allometry for river environments from Randall *et al.* (1995) for freshwater fishes:

$$(10) \qquad API = e^{-13.28} \cdot TL^{2.904}$$

where TL is the average total length in mm.

The API for each age class was estimated from equation (10) using the geometric mean of lengths at the endpoints of each class as predicted by the fitted von Bertalanffy growth curve. An MAPV for each stage was estimated from equation (9), and the MAPV for the entire population was estimated by summing across all age classes.

To explore the effects of limited resource (e.g., habitat, food, etc) availability on extinction probabilities and recovery times we incorporated resource limitation parameters into the matrix model and simulations. This model (Minns 2003) assumes that if the available resources (A_j) exceed the total required resources (a_j) then survival is independent of the resource supply. If, however, required resources are greater than the resources available, the survival of each age-class is reduced linearly in proportion to the ratio between available and required resources. Specifically, survival (s_j) is multiplied by

$$(11) \qquad h_j = \begin{cases} A_j / a_j & \text{if } A_j < a_j \\ 1 & \text{if } A_j \geq a_j \end{cases}.$$

The amount of a given resource required by each individual was calculated based on size in the same ratio as API above. In these simulations, required resources (a_j) were calculated at each time step and summed over all individuals. Results can be interpreted as not only the effects of resource availability, but also resource quality. For instance, doubling the amount of available habitat would be the same as improving the quality of the current habitat two-fold.

RECOVERY STRATEGIES AND TIMES

We used recovery targets to determine recovery timeframes of individual populations under three hypothetical recovery strategies. Since it is likely not possible to direct efforts toward individual vital rates, we focused on positive changes in annual survival probability in early life (i.e., $s_{1,2}$), in adults ($s_{3,4}$), or in fertility ($f_{2..4}$) that might result from specific recovery actions (e.g., the rehabilitation or enhancement of habitat). Specifically, each strategy consisted of improving the associated vital rates by either 10% or 20% to demonstrate the relative performance of investing in different recovery actions.

Initial population sizes for recovery projections were set at 10% of the MVP. As above, the initial population was distributed among age classes according to the stable age distribution. For each recovery strategy, we calculated the probability of recovery in a similar manner to the recovery targets, drawing projection matrices based on a geometric mean growth rate of 2.3 for simulations of the status quo (recovery in the absence of improvement or harm). For each strategy the means of the associated vital rates were increased by 10% (or 20%) before randomly generating projection matrices. We then used 3 000 realizations of population size over 100 years to generate a cumulative distribution function for the time to reach the recovery target, and averaged the results over five runs. The probability of recovery at time t was equal to the proportion of realizations of population size that met or exceeded the recovery target at time t. Simulations both with and without resource restrictions are compared. When a 95% probability of recovery could not be achieved due to insufficient resources, the long term probability of a population being at a recovered level is reported.

RESULTS

ALLOWABLE HARM

Based on the mean vital rates of the Western Silvery Minnow as described above, we estimate the population growth rate of this species to be $\lambda = 2.3$. Elasticity analysis showed that the growth rate is most sensitive to perturbations to early life survival ($s_{1,2}$, Figure 2), and to fecundity of first time spawners. Although the means of deterministically and stochastically determined elasticities are nearly identical, elasticities are still sensitive to stochastic variation (see error bars in Figure 3). Comparing correlations among vital rates and elasticities shows that the uncertainty in these elasticities can be largely attributed to uncertainty in the estimate of age-0 survival. Variation in age-0 survival also explains 82% of the variation in the population growth rate.

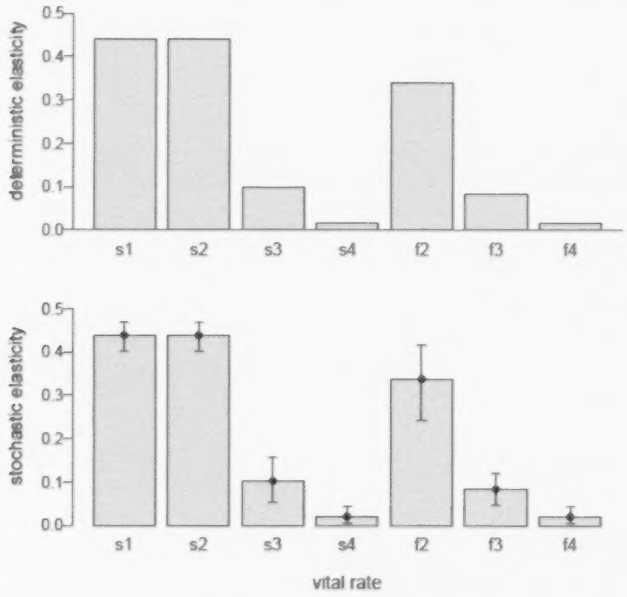


Figure 3. Results of the deterministic and stochastic perturbation analysis showing elasticities (ε_v) of the vital rates: annual survival probability of age j-1 to age j (s_j) and fertility (f). Stochastic results include associated bootstrapped 95% confidence intervals.

Estimates of the maximum allowable harm to vital rates depended on the stochastic element (e.g., mean or upper or lower 95% CI; Table 2). Whenever elasticity based estimates of allowable harm resulted in a population growth rate < 1 (i.e., the approximation was an overestimate), manual perturbations were performed to determine true allowable harm. From a precautionary perspective (i.e., assuming an upper 95% CL), our results suggest a maximum allowable reduction of 60% to juvenile survival (simultaneous harm to ages 0 and 1) or 50% to survival of all ages. Allowable harm for fecundity was determined by manual perturbation to be 86%. If human activities are such that harm exceeds just one of these thresholds, the future survival and recovery of individual populations is likely to be compromised; simulations suggest that recovery time can be severely delayed by levels of harm *below* the maximum allowable harm suggested in Table 2 (Figure 4).

Table 2. Summary of maximum allowable harm ($\tau_{v,max}$) estimates for combined vital rates of Western Silvery Minnow, based on a stochastic perturbation analysis and a population growth rate (λ) of 2.3 (left set) or 1.7 (bi-annual decline in abundance of 50%; right set). s_j = juvenile survival (age 0 to maturity); s_a=adult survival (maturity to age 4); s_n=survival of all ages; f=fecundity. Allowable harm calculated using manual perturbations is also shown. Consistent with the precautionary approach, bold values indicate the recommended maximum allowable harm.

	growth rate: 2.3					Bi-annual catastrophe				
	s_j	s_a	s_n	f	All	s_j	s_a	s_n	f	All
Deterministic mean	-0.64	-4.84	-0.57	-1.29	0.40	-0.48	-3.61	-0.42	-0.96	0.29
Stochastic mean	-0.65	-4.72	-0.57	-1.3	0.40	-0.48	-3.50	-0.42	-0.96	0.29
+ 95% CI	**-0.61**	**-2.85**	**-0.50**	-0.98	**0.34**	**-0.45**	**-2.11**	**-0.37**	-0.73	**0.25**
- 95% CI	-0.71	-9.59	-0.66	-1.91	0.49	-0.53	-7.12	-0.49	-1.42	0.36
manual perturbation	-0.63	-1.00	-0.56	**-0.86**	0.44	-0.47	-1.00	-0.42	**-0.72**	0.31

Allowable harms should be reduced considerably if new evidence suggests a population growth rate below 2.3. It is possible, for instance, that sampled data used to estimate mortality were collected in two "good" years, and that the true variation in survival (and thus in population growth) was not represented, resulting in an overestimation of growth rate and of allowable harm. Table 2 shows allowable harms under the alternative scenario that catastrophic decline (due to drought or some other factor) occurs every two years, but that populations were not sampled in these years. In this case, survival would be 25% lower than our estimates, the population growth rate would be 1.7, and allowable harms are considerably reduced.

RECOVERY TARGETS

Probability of extinction decreases as a power function of population size (Figure 4). Functions of the form $y = a \cdot x^{b}$ were fitted, using least squares and the logged values of *x* (population size) and *y* (extinction probability), to the simulated extinction probabilities for each catastrophe scenario.

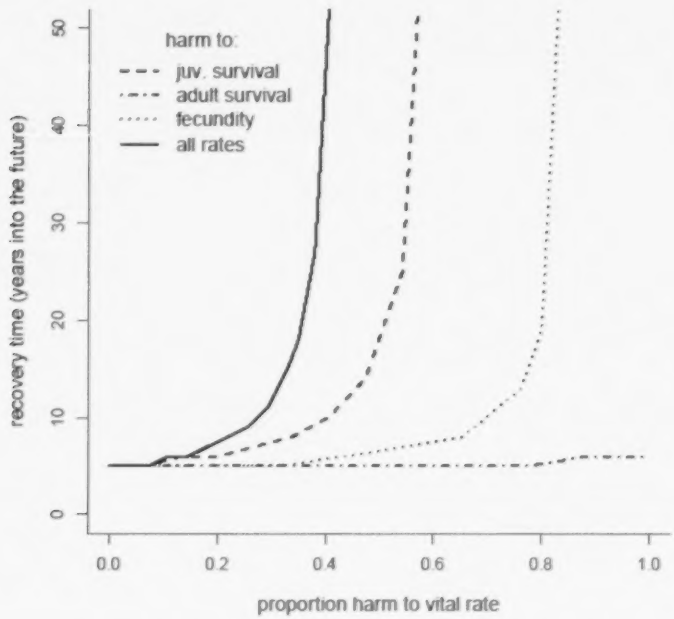


Figure 4. Predicted change in the time to 95% chance of recovery of a Western Silvery Minnow population that is experiencing increased harm to juvenile survival ($s_{1,2}$), adult survival ($s_{3,4}$), fecundity (f), or all vital rates simultaneously. Recovery times are shown as a function of the proportion reduction to each vital rate(s). See Table 2 for maximum allowable harm values.

While choosing a larger recovery target will result in a lower risk of extinction, there are also costs associated with an increased target (increased effort, time, etc.). When determining MVP from the fitted power curves, we attempted to balance the benefit of reduced extinction risk and the cost of increased recovery effort with the following algorithm. (i) We assumed that the maximum allowable risk of extinction is 10% based on COSEWIC's quantitative criteria (E) that a risk of extinction greater than or equal to 10% within 100 years constitutes Threatened status. We define a maximum MVP (i.e., maximum feasible effort) to be the population that would result in a 0.1% probability of extinction, as this is the most stringent criteria in the literature; (ii) using these as boundaries, we calculate the average decrease in probability of extinction per individual increase in population size; (iii) we choose as MVP the population size that would result in this average (i.e., the point on the power curve at which the slope equals the average decrease in extinction risk per increase in target). This represents the point between the upper and lower boundaries where the reduction in extinction risk per investment in recovery is maximized. Calculated in this way, MVP was 1800 adults aged 2-4 (range: 1500–2600 adults) when the probability of catastrophic decline (50%) was assumed to be 10% per generation. If catastrophes occurred at 15% per generation (~6% annually), MVP was 12 000 adults (range: 7000–21 600). In both scenarios, the probability of extinction for the respective MVPs was approximately 0.01 over 100 years (Figure 5). Extinction risk, P(ext.), for the 15% per generation catastrophe scenario can be defined as a function of initial population, N, as:

$$P(ext.) = 22.4 \cdot N^{-0.818}. \quad (12)$$

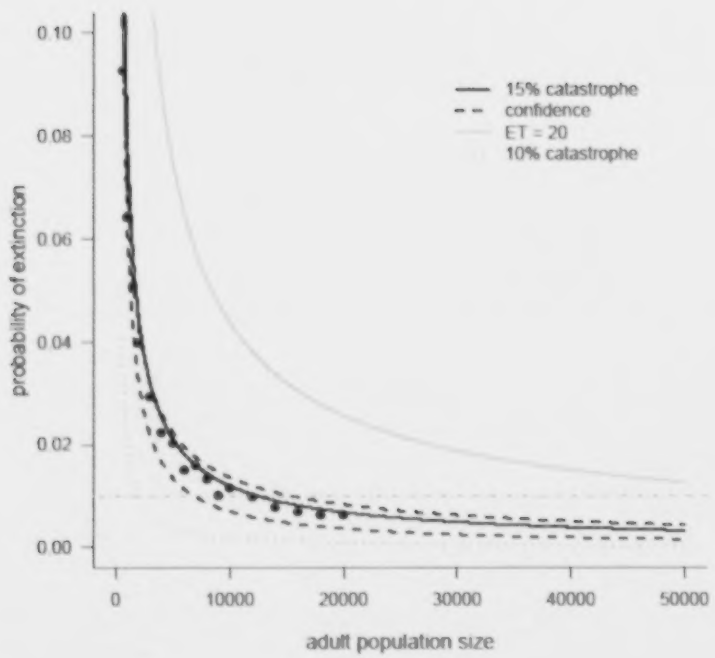


Figure 5. Probability of extinction within 100 years of 10 simulated Western Silvery Minnow populations, at equilibrium, as a function of population size. Black curves assume a 15% probability of catastrophic decline (solid = mean, dotted = max and min of 10 runs), and an extinction threshold of 2 adults. Grey curves represent 10% probability of catastrophe (dotted), or 15% probability of catastrophe and an extinction threshold of 20 adults. Dashed horizontal reference line is at 0.01 and intersects curves at the associated MVPs (Table 3).

MVP simulations assumed an extinction threshold of one adult female (or two adults). We observed that assuming a higher, quasi-extinction threshold (i.e., if the population is considered effectively extinct before it declines to 1 female) results in a linear increase in MVP. If the quasi-extinction threshold is defined as 20 adults, and the chance of catastrophe is 15% per generation, MVP increases from 12 000 to 86 000 adults. An extinction threshold of 50 adults results in an MVP of 236 000 adults. Thus, if the true extinction threshold is greater than one adult female, larger recovery targets should be considered. The relationship between MVP and extinction thresholds (ET) larger than two, for a catastrophe probability of 10% or 15% per generation, can be approximated respectively as

(13a) $MVP_{10\%} = 705 \cdot ET - 1131$

(13b) $MVP_{15\%} = 4985 \cdot ET - 12883$

RECOVERY TIMES

Under current estimated conditions, and in the absence of recovery efforts or additional harm, a Western Silvery Minnow population was predicted to increase from ~1200 adults to the MVP target of 12 000 adults in approximately nine years. This simulation assumed bi-annual catastrophic events (i.e., assuming a population growth rate of 1.7, consistent with the second set of allowable harms in Table 2). Simulated recovery strategies decreased recovery times as much as three years (Figure 6). The most effective simulated strategy was an improvement to

survival of immature individuals ($s_{1,2}$). Consistent with elasticity results, improvements in adult survival had almost no effect on recovery.

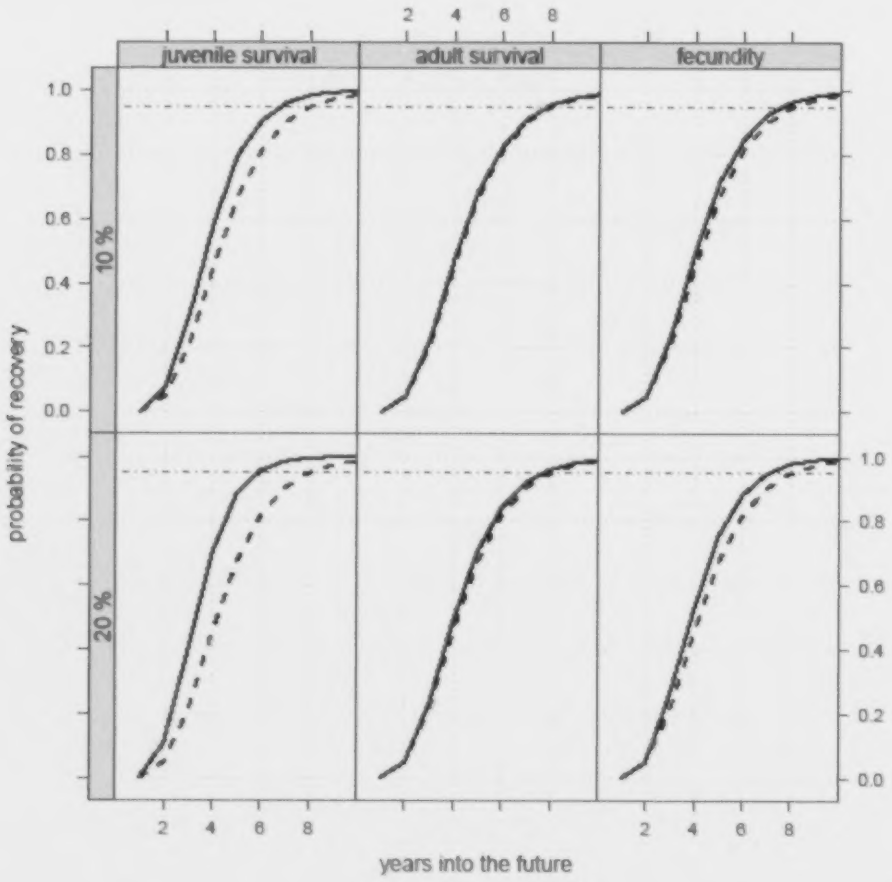


Figure 6. The probability of recovery of 10 simulated Western Silvery Minnow populations under 3 hypothetical recovery strategies and 2 degrees of improvement, based on an initial adult population size that was 10% of the recovery target (1200 adults). Dashed lines show recovery under status quo conditions, assuming no harm, a population growth rate of 1.7, and an annual probability of catastrophe of 50% per generation. Solid lines represent improvement of 10% or 20%, to early survival ($s_{1,2}$), adult survival ($s_{3,4}$), or fecundity ($f_{2,4}$).

MINIMUM AREA FOR POPULATION VIABILITY

The stable stage distribution for Western Silvery Minnow is 99.81% YOY, 0.14% age 1, and 0.04% adult individuals (ages 2-4). With a target MVP of 12 000 adults, under a 0.15 probability of catastrophe per generation, a population of this size was predicted to require 25.3 ha of suitable habitat (Table 3). This area assumes that each individual requires the areas listed in Table 3, and does not account for any overlapping of individual habitats (sharing) that may occur.

Table 3. Stable stage distribution (percentage of the population in each stage), area per individual (API), number of individuals for each age class to support a minimum viable population (MVP) and the resulting estimate of required habitat for each stage and for the entire population (MAPV). Results for three different extinction thresholds and two probabilities of catastrophe are shown.

				Catastrophe = 10%		Catastrophe = 15%	
Extinction Threshold	Age class(es)	Distribution (%)	API (m^2)	MVP	MAPV (ha)	MVP	MAPV (ha)
2	0	99.814	0.008	4.3×10^6	3.4	28.4×10^6	22.6
	1	0.144	0.37	6 137	0.2	40 999	1.51
	2-4	0.042	0.86-1.50	**1 800**	0.2	**12 026**	1.19
	Total				**3.8**		**25.3**
20	0			30.6×10^6	24.4	205.1×10^6	163.2
	1			44 214	1.6	295 979	10.9
	2-4			**12 969**	1.3	**86 817**	8.6
	Total				**27.3**		**182.7**
50	0			80.6×10^6	64.1	558.3×10^6	444.3
	1			116 319	4.3	805 829	29.7
	2-4			**34 119**	3.4	**236 367**	23.3
	Total				**71.8**		**497.3**

Recovery and Extinction with Habitat Limitations

The estimated available habitat for Western Silvery Minnow is 699 ha, which is ample space to support the target population size. There is, however, a serious threat of habitat loss through degradation or fragmentation. We therefore explored scenarios in which (i) some resource becomes limiting, such as a particular type of habitat (e.g. preferred spawning and young-of-the-year habitats are unknown and could be limiting), or (ii) the quality of current habitat is reduced (e.g. low flow). We performed simulations in which Western Silvery Minnow had available varying amounts of resources, and experienced associated density dependence.

When resources were limited, both probabilities of persistence and times to recovery were affected. A population at MVP (12 000 adults), experiencing 15% chance of catastrophe per generation, and having available the minimum required resource quantity and quality (i.e., 25.3 ha of suitable habitat) had a 98% probability of persistence over 100 years. This was only slightly lower than the 99% probability of persistence observed in simulations that did not include resource restrictions or density dependence. If resources were reduced below the minimum level, however, extinction risk increased exponentially (Figure 7).

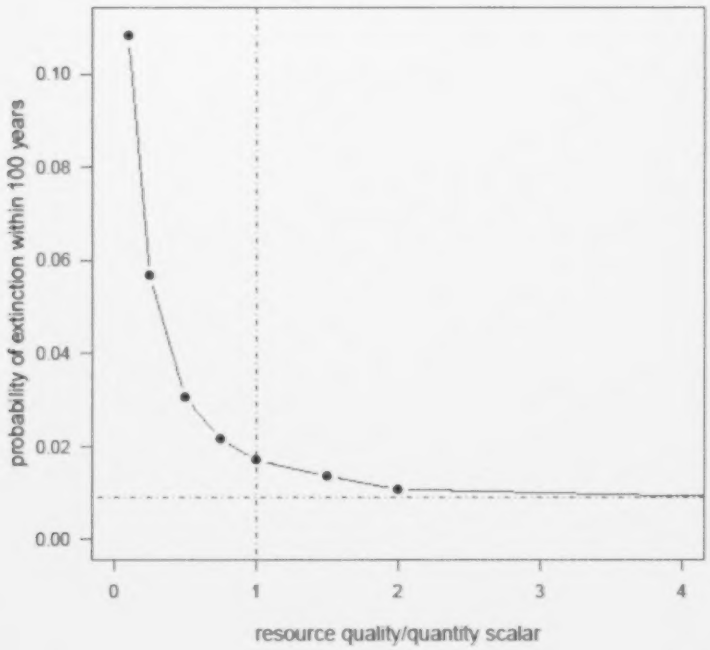


Figure 7. Probability of extinction within 100 years of 10 simulated Western Silvery Minnow populations at minimum viable population (MVP) size, and experiencing resource based density dependence, as a function of a resource availability or quality scalar. Simulations assume a 15% chance of catastrophe. Dashed reference lines show the probability of extinction in the absence of resource restrictions (0.01, horizontal), and the minimum resource quality/quantity (example: Minimum Area for Population Viability, MAPV; vertical).

Resource limitations also reduced the ability of the population to recover. If the amount/quality of resources required for a recovered population exceeded the available resources, simulated populations reached "recovery" abundance occasionally, but did not remain at that abundance due to density dependence (Figure 8). Figure 8 shows the median and 95% confidence intervals (based on 15000 simulations) of population size over time assuming either minimum resource quantity and quality, or 1.5 times this minimum. Also shown is a sample population and its 100 year trajectory. The proportion of simulated populations which were larger than the recovery target (on average over the long term) is shown in Figure 9. At minimum resources, the median population abundance over all simulations was 13 400 adults (~10% larger than MVP; Figure 8), but there was approximately 12% chance of the population abundance being below MVP at any given time (Figure 9). Decreasing resources caused the probability of a population being "recovered" to decrease exponentially, but increasing the availability or quality of the resource by 50% reduced the probability of being below MVP to < 5% (Figure 9).

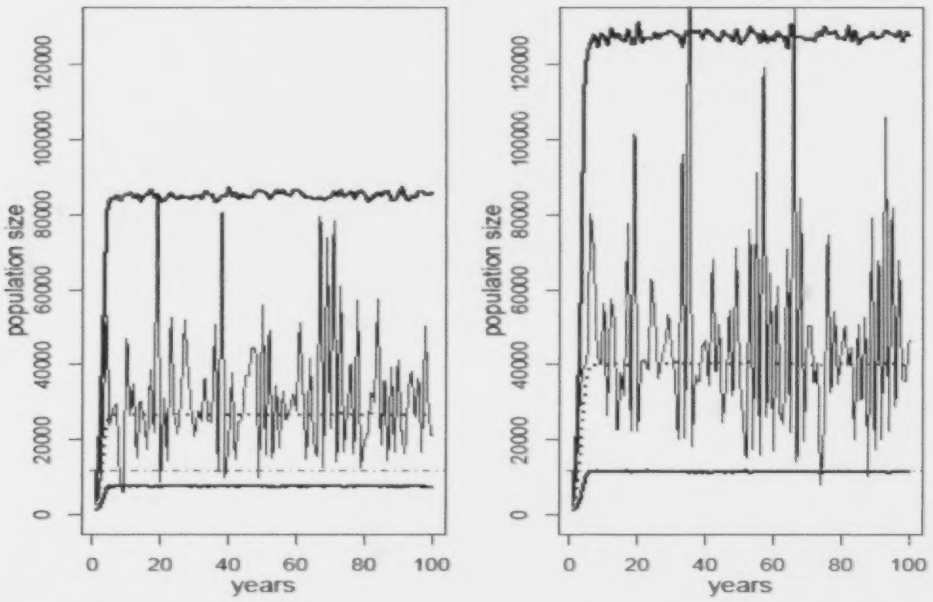


Figure 8. Population size over time of Western Silvery Minnow populations experiencing density dependence, and 15% per generation catastrophic decline. An example population (narrow solid line), and mean (dotted line) and 95% confidence interval (solid thick lines) of 15 000 simulated populations are shown. Horizontal reference line is at the minimum viable population size (MVP). Simulation assumed minimum resource quantity and quality (e.g., Habitat was at the Minimum Area for Population Viability, MAPV; left panel), or at 1.5 times minimum resource quality/quantity (right panel).

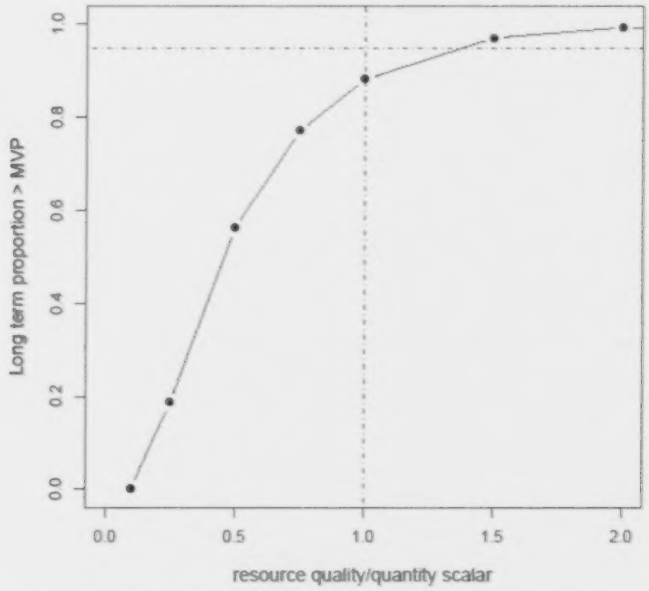


Figure 9. The long term probability (over 15 000 100-year projections) of population abundance being above MVP (12 000 adults), as a function of a resource availability/quality scalar. 15% per generation probability of catastrophe was assumed. Reference lines are at 95% probability of recovery (horizontal), and the minimum resource quality/quantity (e.g. Minimum Area for Population Viability, MAPV; vertical).

DISCUSSION

Our results show that to avoid jeopardizing the survival and future recovery of Western Silvery Minnow, human-induced harm to early life survival as well as the reproduction of first time spawners should be minimal. Harm to any of these life stages is expected to compromise the future survival and recovery of the species. Furthermore, recovery time is expected to be delayed exponentially as harm approaches these thresholds. It is important to note that these estimates of allowable harm assume that the population growth rate before harm (λ) is 2.3. If research indicates that any of our parameters are overestimated, the reduced population growth rate will both lower the scope for harm and produce longer times to recovery.

In addition to providing estimates of allowable harm, this work also provides recovery targets based on the concept of MVP. These targets were estimated at 1800 or 12 000 adults when the probability of a catastrophic (50%) decline (P_k) was 0.10 or 0.15 per generation respectively, and with an extinction threshold of 2 adults. Increasing the extinction threshold to 20 adults increases the MVP to 86 817 adults, and a threshold of 50 adults results in an MVP of 236 367 adults. A threshold of 50 adults is recommended in the literature for maintenance of genetic diversity (Simberloff 1988). According to Reed *et al.* (2003), catastrophic events (a one-time decline in abundance of 50% or more) occur at a probability of 0.14 per generation in vertebrates. We therefore recommend recovery targets based on at least a 15% probability of catastrophe, but suggest that data be collected to confirm the frequency and severity of catastrophic decline experienced by Western Silvery Minnow. Recovery targets based on MVP can be easily misinterpreted as a reference point for exploitation or allowable harm (Beissinger and McCullough 2002). A recovery target is neither of these things because it pertains exclusively to a minimum abundance level for which the probability of long-term persistence within a recovery framework is high. Therefore, abundance-based recovery targets are particularly applicable to populations that are below this threshold, and are useful for optimizing efforts and resources by selecting those populations that are in the greatest need of recovery.

Our analyses show that, in the absence of recovery efforts or harm, and assuming a bi-annual catastrophic decline, a population with an abundance at 10% of the recovery target has a 95% probability of reaching that target in 9 years, provided there is ample suitable habitat available. Additional harm will delay the recovery of a population, with the severity of the delay being related to the sensitivity of the vital rate being harmed. To reduce recovery times, we recommend recovery actions that increase the annual survival rate of immature Western Silvery Minnow; efforts to improve adult survival or fecundity by a similar proportion are expected to be much less effective.

Model results suggest that a recovered population of Western Silvery Minnow requires 25.3 ha of suitable habitat. In addition to this minimum area, Western Silvery Minnow likely require a minimum length of open river for spawning. Western Silvery Minnow belong to the pelagic-spawning reproductive group (pelagophils); drifting eggs are transported downstream, and are vulnerable to increased mortality if they reach standing water and sink (as in a reservoir) before reaching the free-swimming stage (Dudley and Platania 2007). Dudley and Platania (2007) found that palgophils were extirpated from all reservoirs and from nearly all fragmented reaches <100 km in the Rio Grande Basin, suggesting that at a minimum, pelagophils require 100 km of continuous habitat. The Western Silvery Minnow occurs in 310 km of open river, but the distance that eggs will be transported depends on their rate of development and the flow rate of the Milk River, which may differ from rates found in the Rio Grande Basin. We recommend that these variables be determined for Western Silvery Minnow in the Milk River to ensure that age-0 mortality is not elevated by river fragmentation. In simulated populations, insufficient quality or quantity of habitat or other resources increased the extinction risk exponentially, and delayed recovery indefinitely. Simulations also showed that if populations are experiencing density

dependence due to resource restrictions, then an increase in the limiting resource of 50% is required to ensure that the population remains above the MVP target. Note that MAPV estimates do not account for habitat that is shared by different life stages.

Abundance estimates were not available for the Western Silvery Minnow, but have been calculated for a similar species, the Plains Minnow, in a smaller system as 571 fish per km of river. If Western Silvery Minnow is found at the same density, and if it occupies its entire available habitat at this density, then there are approximately 40 000 adult Western Silvery Minnow in the Milk River. If these assumptions hold, then the abundance of Western Silvery Minnow could currently exceed the MVP target of 12 000 adults.

UNCERTAINTIES

We emphasize the need for research on Western Silvery Minnow in Canada to determine (i) survival rates during early life, and (ii) the frequency and extent of catastrophic events for this species.

In lieu of direct estimates of survival of immature individuals our analysis assumed that a size-dependent mortality schedule was appropriate. Ideally, recovery modelling should be based on the life history characteristics of the populations to which they are applied. Uncertainty in age-0 survival had a relatively large impact on both the population growth rate and elasticity values, and consequently strongly influenced allowable harm recommendations. The range of population growth rates achieved in stochastic simulations was very wide (0.92–6.5) and included $\lambda=1$. Therefore, if the true values of some (or all) vital rates are in the lower ranges of their confidence intervals, then populations could be experiencing slower growth than suggested above, and may even be in decline. More accurate estimates of uncertain vital rates are needed to confirm the status of the Western Silvery Minnow population. In lieu of early-life survival estimates, we stress the importance of determining the true population growth rate.

The choice of the recovery target is impeded by a lack of information regarding catastrophic events; targets and model predictions vary widely depending on the frequency of catastrophic decline in the population. Research that identifies the magnitude and frequency of catastrophic events will greatly reduce the uncertainty in estimates of minimum viable population size, and thus in recommendations for the conservation of Western Silvery Minnow in Canada.

Finally, predictions from this model assume random mating and complete mixing of the population (i.e., all individuals interact and can reproduce with one another). This assumption should be considered when applying MVP targets, and larger targets should be set if the assumption does not hold. A further consideration is that MVP targets suggested above assume an extinction threshold of 1 adult female. If a higher true extinction threshold is likely, we suggest that a larger target be set using equation (13).

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